# THE INFLUENCE OF SEASONAL ENVIRONMENTAL CHANGES UPON THE METABOLISM, LETHAL TEMPERATURE AND RATE OF HEART BEAT OF GAMMARUS LIMNAEUS (SMITH) TAKEN FROM AN ALASKAN LAKE

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Fresh water biological studies in Alaska have until quite recently been conducted mainly by scientists visiting the Territory during the few summer months. Consequently very little has been known about the conditions under which the fresh water fauna exist throughout the seasons. Prolonged winter cold, brief summer warmth and the restrictions of the habitat caused by the dehydrating effect of extensive winter freezing are environmental factors not encountered by aquatic life in temperate regions. These conditions, however, bring out a number of problems of considerable basic scientific interest.

It has therefore been the plan of this study to examine the metabolic rate of the amphipod crustacean *Gammarus limnaeus* (Smith) for evidence of adaptive adjustments to the extreme seasonal changes typical of Alaska for comparison with the adaptations to temperature shown by aquatic animals from other regions. *Gammarus limnaeus* (Smith) was selected as a suitable subject for this study because of its wide distribution in Alaska, its importance as a fish food, and its consequent significance as a link in the chain of reproduction in fresh water. Its close taxonomic relation to other amphipods abundant in much of the northern world facilitates comparison.

*Gammarus limnaeus* (Smith) belongs to the genus *Gammarus* (Fabricius) and the amphipod family Gammaridae. The genus is very widely distributed in both salt and fresh water. Over 30 species are known, and of those 6 are found in North America, *Gammarus limnaeus* together with *Gammarus fasciatus* being the most common and widely distributed of the northern species; both occur in Alaskan lakes and ponds. *Gammarus limnaeus* is found throughout the United States from Maine to New Mexico (Weckel, 1907). Related species are common in fresh water throughout Siberia and Northern Europe.

## PREVIOUS INVESTIGATIONS

The underlying proposition for this study was first expressed by Krogh (1916, p. 101): "One would expect that animals living at a very low temperature should show a relatively high standard metabolism at that temperature compared with others living normally at a high temperature." The abundance and activity of life in cold northern waters in which poikilotherms from warmer waters would be in-

jured or slowed to ineffectiveness by cold is in good agreement with this basic statement.

Considerable information is available on the reaction of poikilotherms to changes in temperature and oxygen tension during experiments in the laboratory. Less attention, however, has been given to the matter of determining 1) whether certain physiological adjustments of transitory or more permanent nature take place in cold blooded animals when in their natural surroundings, and 2) to what extent these adjustments might help the animal overcome changes in the environment that otherwise could have an adverse effect upon its success in living in the habitat.

Although only a few investigations seem to have been specifically directed toward the detection of seasonal or local variation in the metabolism of aquatic poikilotherms, it is not uncommon to find references to such differences in the temperature-metabolism relation of cold blooded animals. Cronheim (1911) considered that analysis of Knauthe's (1898) experiments with carp showed seasonal variation in metabolic rate. Wells (1935) found that the Pacific killifish (*Fundulus parvipinnis*) showed variations in its metabolic rate during the year and connected the fluctuations with the yearly changes in temperature of the waters in which they lived. Bruce (1926) carried out a year's study on *Mytilus edulis*, and found a seasonal variation in the oxygen requirement of this species which he associated with the reproductive cycle. Haugaard and Irving (1943) found such small seasonal variations in the oxygen consumption of the cunner (*Tautogolabrus adspersus* Walbaum) that the slightly higher oxygen consumption in winter than in summer at each temperature below 15° C. appeared too small to be regarded significant as an adaptation. In the sand crab (*Emerita talpoidea* Say), Edwards and Irving (1943) found a change in the relation of oxygen consumption up to four times higher in winter at 30° C. than in summer. The higher oxygen consumption rates in winter they interpreted as an adjustment by means of which the animals sustained activity and growth at the low winter temperatures.

Variation in the metabolism and such related functions as heart beat and pleopod movements in animals apparently identical systematically but taken from different latitudes has been reported by several authors, *viz.* Fox (1936, 1938, 1939), Fox and Wingfield (1937), Wingfield (1939), Spärck (1936) and Thorson (1936). The general assumption has been that the different temperatures of the two environments are responsible for the differences observed between the two groups in physiological response to changes in temperature during the experiment.

Marshall, Nicholls and Orr (1935) found seasonal differences in heat tolerances of *Calanus finmarchicus* with elevation of the lethal temperatures from 24° C. winter to 26° C. summer.

Hörstadius (1915) noted the point of normal development for *Paracentrotus lividus* eggs and found it to vary with the season. Runnström (1936) noted similar adjustment of both the upper and the lower limits for the development of the tunicates *Ciona intestinalis, Phallusia mammillata* and *Ascidia mentula,* and the sea urchins, *Paracentrotus lividus* and *Arbacia aequituberculata.* Fry (1947) in his paper on the effects of the environment on animal activity gives an extensive review of the existing literature in this field, in which he points out the importance of considering the environmental factors in physiological research and discusses the problems of acclimatizations.

Scholander, Flagg, Walters and Irving (1953) reviewed the literature of adaptation to cold and from their own observations compared the metabolism of arctic and tropical animals, including in their list terrestrial as well as aquatic poikilothermic forms. A general summary of their findings was that arctic aquatic forms in their accustomed temperature near 0° C. maintained a metabolic rate $\frac{1}{3}$ to $\frac{1}{10}$ as great as the tropical forms in their usual temperature of 30° C. If, however, the metabolic curve of the tropical forms is extrapolated down to 0° C. it represented only $\frac{1}{30}$ to $\frac{1}{40}$ of their metabolism in their tropical environment. Arctic forms showed a considerable, although not complete, adjustment of metabolism to their environment. In terrestrial forms, on the other hand, practically no such adjustment appeared (Scholander *et al.,* 1953).

The previous findings and reports thus all indicate the ability of aquatic poikilotherms to adjust themselves to their surroundings and also show the necessity for taking into consideration the original environment of the test animals in physiological experiments. From these former findings it could be expected that the amphipods from an Alaskan lake would show a higher oxygen consumption at a given low temperature in winter than in summer, with a higher metabolism that could facilitate a higher rate of growth in the winter months than would be expected from their temperature-metabolism relation in summer. In order to regard physiological processes as adaptive it is of prime importance to refer them to the conditions of the animal's natural environment and their behavior during the cycle of the seasons.

<center>MATERIAL</center>

The animals used in the experiments were all taken from Goose Lake, an eutrophic-type lake about two miles south of Anchorage, Alaska, averaging about eight feet in depth and covering about 30–40 decares. The margins of the lake are swampy, and there is no definite inlet or outlet. The banks contain deposits of peat over gravel and the bottom of the lake consists of a 1½-foot deep layer of mud and decomposing material, a so-called false bottom underlain by a base of glacial gravel. In summer the lake has a rich vegetation of water lilies, *Nymphaea,* and other water plants, with water temperatures rising to more than 20° C. In winter the lake freezes to a depth of about 3–3½ feet or more. It is doubtful, however, that it ever freezes to the bottom. Ice is on the lake from the middle part of October to the first part of May.

The animal life of the lake is surprisingly rich, with many insect larvae and a number of crustaceans including many cladocera and smaller numbers of amphipods and copepods. Snails, leeches, flatworms, and mites are also common. In winter the amphipods seem more abundant and a smaller number of cladocera and copepods are present. Whirligig beetles (Gyrinidae), boatmen (Corixidae), and water beetles (Dysticidae) are found as adults, and snails, flatworms, leeches, and the larvae of dragonflies (Aeshnidae), and damselflies (Agrionidae), are commonly found on the bottom.

Only one species of amphipod was found, *Gammarus limnaeus* (Smith), described by S. I. Smith (1874). The animals were present in the lake in fairly large numbers throughout the year. The main breeding season of *G. limnaeus* seems to be shortly after breakup of the ice in the spring. At that time they are abundant

along the shores, where many are found copulating in the shallow water. Some ice may still remain in the middle of the lake. The number of *G. limnaeus* seems to fluctuate through the summer, varying according to location.

The *G. limnaeus* used for study were caught with a dip net from the shore or from a rubber raft in summer, and in the winter through a three-foot square hole in the ice which was allowed to freeze over to keep the water from contact with air. In the laboratory the amphipods were kept in large thermos jars at as near the lake temperature as possible. Animals were usually caught in the morning and observations were started immediately, thereby avoiding prolonged exposure to indoor conditions and significant changes in temperature. The animals used were of various sizes and of both sexes as no significant sex differences in oxygen consumption were observed. Animals infested with parasites, such as acanthocephalid larvae and what was probably a larval tapeworm, were eliminated. All animals carrying eggs or showing low vitality were discarded.

## Experimental Procedure

*1. $O_2$ consumption.* Oxygen consumption was measured by means of Scholander's micro- and semi-micro respirometers (Scholander, 1950). The temperatures in the water baths were kept constant within plus or minus 1° C. During most of the experiments simultaneous runs at four different temperatures, ranging from 0° C. to 22° C., were performed so as to utilize animals with as similar physiological background as possible. Fifteen individuals in separate chambers were used at each temperature and necessary handling was done by means of a pipette so as to avoid damaging the fragile legs or respiratory organs. Filtered lake water was used in the respiratory flasks. Blanks with lake water were run parallel to the experiments in the same water bath. Measurements were timed from several hours up to 24 to secure representative data for the oxygen consumption. Day and night measurements and those conducted inside a dark, walk-in ice box revealed no significant diurnal cycles or influence of light. Data obtained on animals that died during one observation and on those showing low vitality were discarded.

*2. Adequacy of oxygen supply.* Consideration was given to the possible influence of changing oxygen tension upon the metabolic rate of invertebrates, as reported by Amberson, Mayerson and Scott (1924). Analysis of the water from the vials after the termination of the measurements revealed that the animals themselves, by their respiratory movements and activity, stirred the water sufficiently to keep the oxygen content of the shallow water in the vials at more than $\frac{2}{3}$ saturation. Analysis of $\frac{1}{2}$ cm.$^3$ of the water from the respiration vessels was made by means of the Winkler method modified according to van Dam (1935), and conducted inside a syringe. Titration was carried out with Scholander's microburette (Scholander, Edwards and Irving, 1943), using a magnetic stirring device operating as described by Linderström-Lang and Holter (1940).

*3. Weight and composition of specimens.* After the runs the animals were blotted with a filter paper and dried to constant weight without heat in a desiccator with calcium chloride, to determine the water content and the dry weight of the animals. A determination of the hydrolyzable material of the animals was carried out to facilitate comparison with similar figures cited in the literature. For this purpose a group of fifty animals was dried with filter paper, weighed, and dried in a

desiccator in the same way as for determination of dry weight. After weighing, the animals were boiled in 10% KOH for one hour and the residual matter filtered, dried and weighed. Residue, principally chitinous and similar materials undissolved in KOH, might be considered inert in ordinary respiration. The weight of

TABLE I

*Content of water and hydrolyzable material of Gammarus limnaeus (Smith)*

| Date | Wet wt. of 50 animals grams | Dry wt. of 50 animals grams | Water % | Hydrolyzable material of 50 animals grams | Hydrolyzable material of 50 animals % |
|------|------|------|------|------|------|
| 1–9–51 | 1.020 | 0.240 | 79.6 | | |
| 1–15 | 1.010 | 0.215 | 78.8 | | |
| 1–23 | 1.020 | 0.225 | 77.9 | | |
| 3–12 | 0.860 | 0.165 | 80.8 | 0.816 | 14.0 |
| 3–26 | 0.782 | 0.143 | 81.8 | | |
| 3–28 | 0.850 | 0.160 | 81.2 | | |
| 4–2 | 0.922 | 0.167 | 81.8 | | |
| 4–4 | 0.927 | 0.165 | 82.2 | | |
| 4–9 | 1.076 | 0.184 | 82.9 | 1.016 | 11.5 |
| 4–12 | 0.994 | 0.174 | 82.5 | 0.938 | 11.8 |
| 4–16 | 0.975 | 0.165 | 83.1 | | |
| 5–7 | 0.948 | 9.194 | 79.5 | | |
| 5–10 | 0.972 | 0.194 | 80.1 | | |
| 5–16 | 1.067 | 0.199 | 81.3 | | |
| 5–24 | 1.057 | 0.214 | 79.8 | | |
| 6–7 | 1.126 | 0.233 | 79.3 | | |
| 6–11 | 1.035 | 0.195 | 80.1 | | |
| 6–21 | 1.465 | 0.265 | 81.9 | | |
| 7–10 | 1.025 | 0.207 | 80.3 | | |
| 9–20 | 1.110 | 0.220 | 80.2 | | |
| 9–26 | 1.060 | 0.215 | 79.7 | | |
| 10–8 | 1.237 | 0.240 | 80.8 | | |
| 10–22 | 1.635 | 0.320 | 78.6 | | |
| 11–21 | 1.412 | 0.315 | 79.1 | | |
| 12–6 | 1.390 | 0.257 | 81.5 | | |
| 12–13 | 1.750 | 0.352 | 79.8 | | |
| 12–20 | 1.557 | 0.332 | 78.5 | | |
| 1–9–52 | 2.020 | 0.410 | 79.7 | | |
| 1–17 | 1.377 | 0.281 | 79.5 | | |
| 2–5 | 1.698 | 0.349 | 79.4 | | |
| 4–8 | 1.812 | 0.287 | 84.3 | | |
| Average | | | 80.5 | 0.923 | 12.4 |

the hydrolyzable material was calculated in per cent of wet and dry weight (see Table I). There was no suggestion that this residue changed sufficiently to alter results. The reference of oxygen consumption to wet weight, dry weight or hydrolyzable material should therefore give about the same relationship. The oxygen consumption was most conveniently given per unit wet weight and was chosen as a basis for the figures used in the accompanying tables and graphs.

4. "Lethal" temperature. Determinations of the "upper lethal" temperature at the end of the winter and in the summer were made. The highest tolerable temperatures were determined by suspending small glass vials containing lake water and 5 animals each in thermos bottles filled with water with a temperature difference of 2° C. from 24° C. to 36° C. The vials were checked every 15 minutes and the dead animals were picked out. Paralyzed animals showing no signs of life were counted together with the dead ones even though a few recovered when placed in cold water. Any attempt to distinguish between paralyzed and dead animals would be very difficult and possibly irrelevant. One hundred per cent survival after one hour exposure to a given temperature was used as a standard for determining the animal's level of heat tolerance.

5. Heart rate. The heart beat was counted by means of transmitted light that had passed through a ¾-inch thick layer of flowing water in a specially constructed water-cooled microscope stand (Krog and Simmet, 1954) which permitted temperature control to within plus or minus 0.1° C. The animals were surrounded by lake water during the test. The temperature of the water immediately surrounding the animals was measured by means of a fine thermocouple. Four to five ½-minute counts were taken at each temperature and the average rate of heart beat calculated.

## RESULTS OF OBSERVATIONS AND EXPERIMENTS

*Temperature and oxygen supply in the lake.* The curves in Figure 1 show the yearly variation in temperature and oxygen content of the water in Goose Lake, together with the saturation curve for oxygen dissolved in the water at the recorded temperatures. The oxygen content in the lake reached its lowest values in February and March when it dropped below amounts detectable with the Winkler method used for this determination (Standard Methods for Examination of Water and Sewage, page 724). The summer months give quite steady values for dissolved oxygen. As seen from the curve, the increase of oxygen in the lake starts before the breakup of the ice. This is probably due to accumulation of water from melting snow on the top of the ice, which is later drained into the lake through enlarged cracks. This incident is followed by a lifting of the ice caused by the rising water level and subsequently by appearance of open water along the shores. From this time on, direct contact between the lake water and the air is established, and the $O_2$ content increases gradually.

The water in the lake, however, never reached saturation at any temperature. After the oxygen content reached a value of around 8–9 ppm., it leveled off and remained at that level throughout the summer. The first decrease of oxygen in the lake followed, after some delay, the freeze-up in the fall and it continued to decrease at a fairly even rate in the following months until it reached its minimum in February, March, and April. Reduction of the oxygen supply in winter is probably

common in the shallow lakes of Alaska and might explain why no fish have been found in so many of the smaller, shallow, non-circulated lakes although fish food appears to be abundant.

The temperature of the water in the lake also varied considerably with the season, rising in summer above 20° C. (see Fig. 1). The temperature increased rather sharply in the spring because of the shallowness of the water and the lack of any significant out- and in-flow. The pH was not observed to change consistently with the season and stayed between 7.0 and 8.0.

Variation of the amphipods' oxygen consumption with size was found to occur in the course of the year as is shown when the oxygen consumption at 10° C. is
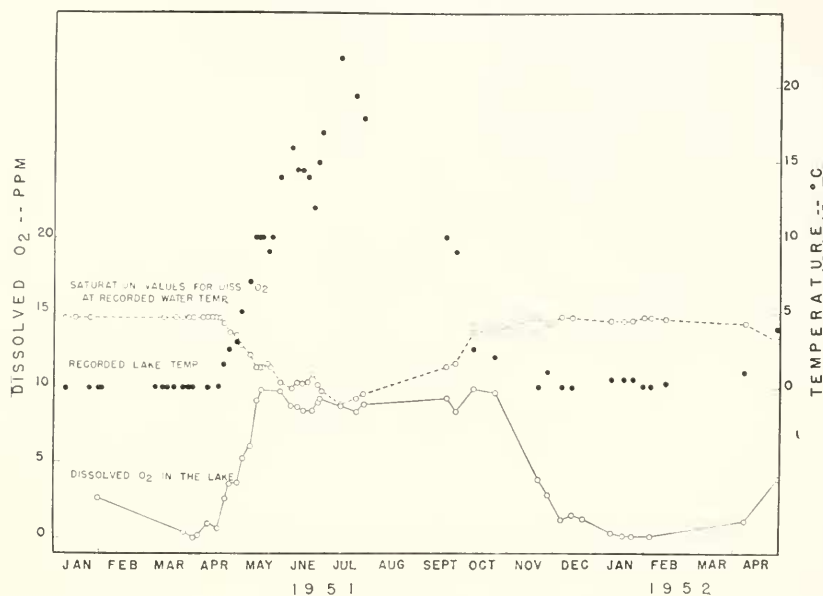


FIGURE 1.  Recorded temperature in Goose Lake 1951 through April 1953, together with calculated saturation values for dissolved oxygen at those temperatures, and actual recorded dissolved oxygen during the same period, measured in parts per million by weight.

plotted against weight (see Fig. 2). Curves plotted at other temperatures show similar although not so pronounced variation. A further breakdown of the data in weight groups was not found desirable as it would complicate the final comparison between summer and winter animals and only slightly improve the spread of the values.

To simplify comparison, the year was divided into two seasons—June and July —(see Fig. 3) representing the typical summer period with fairly high temperatures and rather constant oxygen content of the water, and the late winter—February through March—which is the period of lowest oxygen content, disregarding the transition between these two periods. During the winter period a significant lowering of the oxygen utilization of the animals was found to occur when the oxygen content in the lake water was lowest, suggesting a difference between the

seasonal adjustment in these animals and the Crustacea previously investigated. These have, however, been mainly marine forms or those from well circulated waters with fairly high and stable oxygen tensions and with the temperature as the most important variable.

Figure 4 shows the upper temperature tolerance as determined for the animals in winter as well as in summer. The highest temperature which the animal can tolerate as determined by 100% survival for one hour, seems to be about 26° C. for the winter animals, and for the summer animals from 30°–32° C. This shows a lowering of the resistance to heat by 4°–6° C. in the cold season as compared to the summer, which is about what would be expected from previous investigations of temperature adjustments in invertebrates.
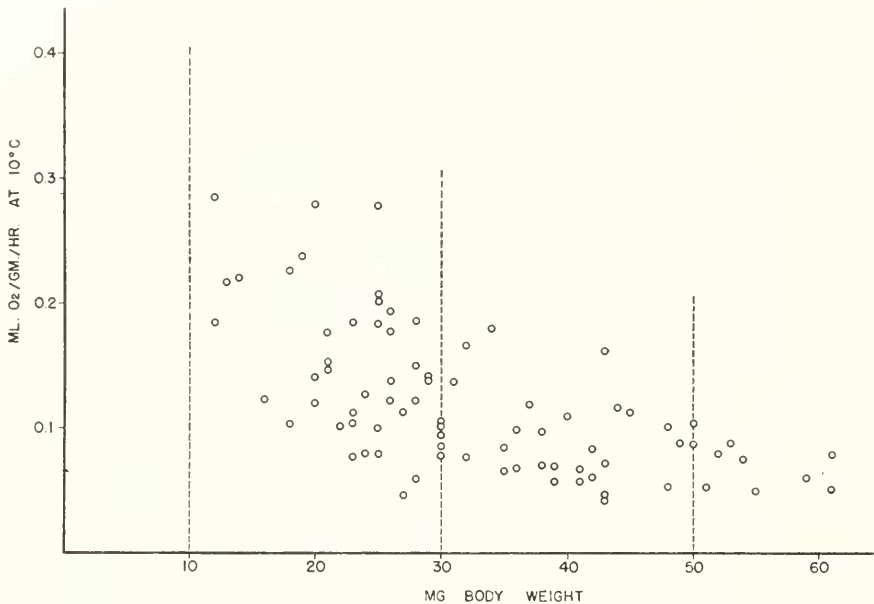


FIGURE 2. Relation between body weight and oxygen consumption at + 10° C.

The pulsation rate of the "heart," or more correctly the dorsal vessel of the animal, was recorded at the end of winter (March) and at the end of summer (the last part of August) in order to determine the extent of seasonal variation. Figure 5 shows the rate of pulsation plotted against temperature. A slight elevation in the relation of heart rate to temperature seemed to occur in winter with generally lower heart rates at all temperatures for the summer animals. Above 19° C. the winter animals were observed to show irregularity in their "heart" beat with an eventual decrease in rate. The larger spread in the data for the winter animals at the higher temperature as compared with the summer animals is believed to be mainly caused by this reaction (see Fig. 5). The summer animals on the other hand showed a normal increase of the "heart" beat above 14° C. up to around 23° C. after which irregularity and consequent gradual drop in heart rate occurred as in the winter animals.

FIGURE 3. The relation between oxygen consumption and temperature in the periods February through March and June through July, plotted on a semilog scale. The animals from the two different seasons are marked with separate symbols.

## DISCUSSION

On the basis of previous studies of the adaptation of the metabolism of aquatic invertebrates to temperature, it was anticipated that animals from an Alaskan lake, with the relatively long exposure to low water temperatures, would show a metabolic adjustment so as to consume more oxygen at a certain low temperature in the winter than at the same temperature in the summer. No such adjustment has been observed in the present study. On the contrary, a decrease in oxygen consumption in February and March can be noticed (see Fig. 3). Although the variation is not
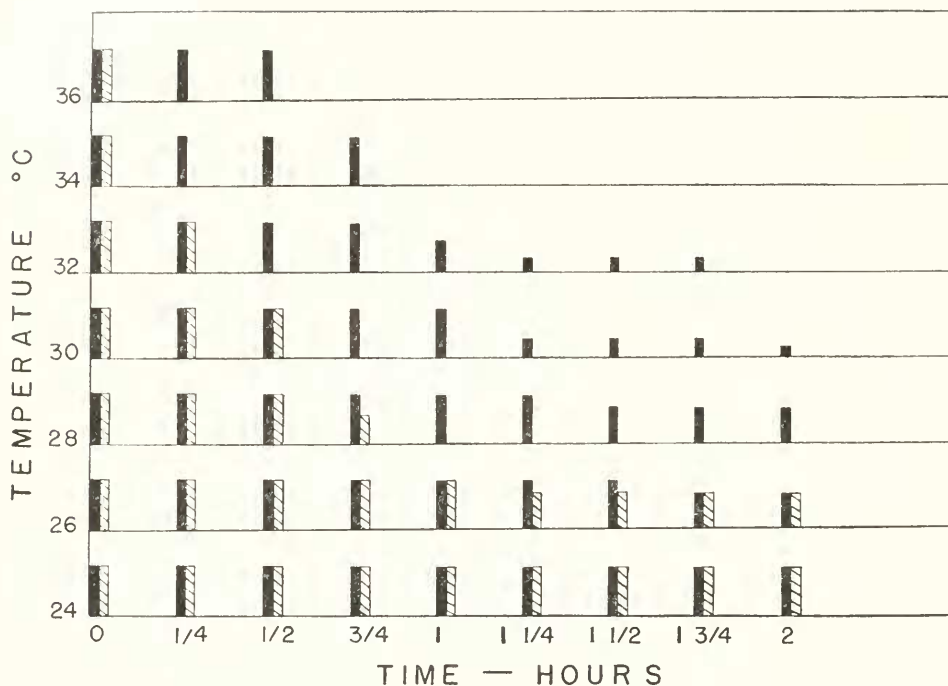


FIGURE 4. Diagram shows upper lethal level of the amphipods respectively in the winter and in the summer. Full length columns at extreme left represent five animals each. Filled columns are summer animals, cross lined are winter animals.

large the constancy and trend of the changes indicate their significance. It will therefore seem natural to connect the low oxygen consumption of the amphipods in late winter with the low oxygen content of the water at that time. Pursuing the same reasoning, the absence of the expected adaptation in metabolic rate to low winter temperatures, as found by investigators in other situations, could be caused by the fact that there is not enough oxygen for such an adaptation to be useful.

Assuming that adjustments made by animals in the face of unfavorable environmental factors are directed toward the factors that are most critical, the differences between previous findings and the situation reported at Goose Lake can be more easily understood. The low oxygen consumption of the animals from Goose Lake

in the late winter might thus be described as a result of a compensatory adjustment in metabolic economy toward the most critical environmental factor at that time. Such an adjustment, although not large, might be of vital importance to the animals, living as they do through long periods with oxygen supplies which must be approaching the lowest limit that they can tolerate and still carry on an aerobic metabolism.

Experimentally induced adjustment to low oxygen content by exposure to environment with low oxygen has previously been reported in the literature. Lund (1921) reported that repeated exposure of *Planaria* to low oxygen tensions caused less increase in oxygen uptake after each experiment. Hiestand and Singer
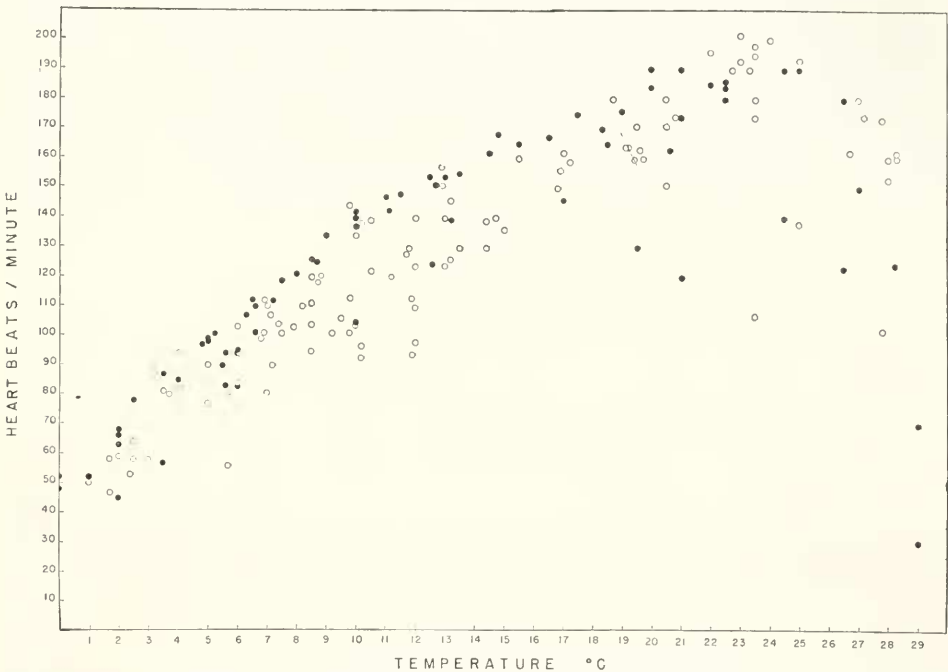
FIGURE 5. Heart rate in beat per minute plotted against time. Open circles represent summer animals and solid dots, winter animals.

(1934) also found that leeches responded by "acclimatization" after repeated exposure to water with low oxygen content, and that they gradually went back to their former state after the experiments were terminated. The question whether these experimentally induced changes in oxygen uptake are comparable with the natural reduction occurring in amphipods cannot be answered but the similarity is striking. On the other hand the benefit of such an adjustment for the amphipods seems quite clear and the remarkable ability of the animals to get along with the low amount of oxygen available in the late winter can be more easily understood. Adjustment to a high oxygen consumption in the winter, such as that reported in literature dealing with other poikilotherms, would in the case of the Alaskan amphipods

be unfavorable as it is of more moment for them to survive the winter than to maintain a high metabolism when the oxygen supply is critically scant.

The $Q_{10}$ as calculated from Figure 3 shows values around 2, the $Q_{10}$ in the winter being slightly lower in value than in the summer (see Table II). Scholander *et al.* (1953) have given a complete discussion of the problem of $Q_{10}$ as an indication of an animal's state of adaptation to the environment. They concluded that physiological adaptation of poikilotherms to cold has its manifestation in the lateral displacement of the metabolism temperature curve but not in the change of its slope as expressed as change in $Q_{10}$. In the amphipods the summer and winter values for $Q_{10}$ did not differ appreciably.

The changes in the upper lethal temperature levels follow fairly closely those expected on the basis of previous reports upon temperature tolerances of poikilotherms, adding no new information regarding this type of adjustment.

The changes in heart beat, although quite small, show on the other hand some rather interesting trends. The differences between the summer and winter rates above 19° C. indicate that the summer animal can increase its heart rate beyond the point at which the winter animal's heart ceases to function normally. The over-all lower heart rate of the summer animal below 20° C. is not easily understood. Fox (1939) found that the marine polychaete worm *Perinereis cultifera* from English

TABLE II

*$Q_{10}$ of $O_2$ consumption in Gammarus limnaeus (Smith)*

| Time | Temperature °C. | | |
|------|:---:|:---:|:---:|
|      | 0–10 | 5–15 | 10–20 |
| Summer | — | 2.4 | 2.0 |
| Winter | 2.1 | 2.1 | 1.8 |

waters had the same rate of heart beat at 14° C. as the same animal from the Mediterranean had at 20° C. He also found that crustaceans from colder waters around the British Isles had, on the average, a higher rate of heart beat at a given temperature than those from warmer waters of the Mediterranean despite the fact that arctic animals are usually bigger than individuals of the same species from warmer waters, and an opposite relationship between size and heart rate seems to exist commonly among invertebrates. The present observation of changes in heart rate according to season within the same animal population could be compared to the findings reported by Fox (1936) on marine invertebrates taken from waters at different latitude and temperature, except that the changes observed in the Alaskan amphipods might be explained as being brought about through adjustments to the yearly variation in the environment. The particular component or components of the environment which induce this reaction, however, cannot be fully determined. A direct parallel to the cases reported upon by Fox, with an apparent relationship between the physiological responses to laboratory-imposed temperature changes and the temperature of the animal's original environment, would only be possible if the oxygen content of the water were plentiful. Under the reported conditions there is also the probability that the heart rate would increase in the winter so as to compensate for the lower oxygen content of the water at that time of year.

This and related studies suggest that considerable physiological flexibility seems to be present in individual aquatic poikilotherms, making it possible for them to make adjustment to comparatively large variations in their environments. The differences between the winter and summer temperature in Alaska equal the difference in the sea around Britain and in the Mediterranan. One population of amphipods encounters the Alaskan seasons by adaptive physiological changes occurring during the life of individuals. Two isolated sections of a population might continue to live safely within the extremes of their physiological adaptability without offering a visible hold for natural selection to differentiate their physiological processes.

It is a great pleasure for me to acknowledge the guidance, interest, and kind criticism by Dr. Laurence Irving during the course of this study. I would also like to thank Miss Mildred Wagner for the excellent help in doing determinations of dissolved $O_2$, and the drawings; my wife, Hildur Krog, for assistance in the calculation of the data; Dr. P. F. Scholander for kindly reviewing the manuscript and for valuable suggestions concerning the presentation of the results, and Dr. Leslie Hubricht for identifying the amphipods.

## Summary

1. A year's cycle of the oxygen consumption of the amphipod, *Gammarus limnaeus* (Smith), has been recorded. The metabolism has been related to the environmental factors encountered in a shallow Alaskan lake, which is ice-covered during seven winter months.

2. A seasonal change in the metabolic rates of the animals accompanied changes in the available oxygen. These resulted in decreased oxygen consumption during the winter when the oxygen supply in the lake was low.

3. The lethal temperature of the amphipods changed from 26° C. in winter to 30°–32 C. in summer.

4. The rate of the heartbeat of the animals varied slightly with the season, with a higher average rate at temperatures below 20° C. in winter than in summer.

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